AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 109:365–386 (1999)

Seed Handling in Chimpanzees (*Pan troglodytes*) and Redtail Monkeys (*Cercopithecus ascanius*): Implications for Understanding Hominoid and Cercopithecine Fruit-Processing Strategies and Seed Dispersal

JOANNA E. LAMBERT*
Department of Sociology and Anthropology, Southwest Missouri State University, Springfield, Missouri 65804-0095

KEY WORDS Kibale National Park, Uganda; frugivory; digestion; guenons; apes

ABSTRACT Primates are confronted with an array of constraints in feeding on fruit, including the removal of adhesive, energy-rich pulp from seeds. In this paper, I discuss how primates meet this challenge and present data on the fruit-processing and seed-handling behavior of chimpanzees and redtail monkeys in Kibale National Park, Uganda. These data are then related to these species' services as seed dispersers. Particular attention was paid to the methods by which primates removed pulp from seeds, the density of seed clumps that they deposited (by spitting, dropping, or defecating) to the forest floor, and the distance seeds were moved from parent trees. Distance and density differences in chimpanzee and redtail seed dispersal resulted from distinct fruit-processing and seed-handling methods. It was observed, in general, that redtail monkeys engaged in fine oral processing and were seed spitters: most seeds were dispersed in close proximity to parent trees (84% of spat seeds $<$10 m of parent tree), and deposited singly (100% seeds spat singly). In contrast, chimpanzees were coarse fruit processors and seed swallowers: seeds were defecated in denser clumps (e.g., a mean of 149 large seeds/dung sample and hundreds of small seeds/dung sample), far from parent trees. I evaluate the factors that shape patterns of fruit processing in hominoids and cercopithecines, and argue that the observed seed handling differences can be attributed to differences in digestive retention times, oral anatomy, and alternative mechanisms by which to avoid the cost of seed ballast. Am J Phys Anthropol 109:365–386, 1999.

Most primates have a diet that is composed, at least in part, of angiosperm fruit. Although there can be considerable inter- and intraspecific variance in the composition of these fruits (Waterman, 1984; Leighton, 1993; Wrangham et al., 1993; Conklin and Wrangham, 1994), the succulent or pulpy components of ripe fruit mesocarp typically contain large amounts of readily assimilated, simple sugars that fulfill energetic requirements (Milton, 1984). In addition to sugars, fruit pulp can also be a source of water, and, less commonly, fat (Nagy and Knight, 1994; Oftedal and Allen, 1996). However, fruit as a resource is not without constraints to a consumer. For example, since most tropical forests are characterized by tree species with seasonal and annual

Grant sponsor: Makerere University; Grant sponsor: University of Illinois Graduate Fellowship; Grant sponsor: Sigma Xi; Grant sponsor: Department of Anthropology, University of Illinois; Grant sponsor: Center for African Studies, University of Illinois; Grant sponsor: Graduate College, University of Illinois.

*Correspondence to: Joanna E. Lambert, Department of Anthropology, University of Oregon, Eugene, OR 97403-1218.

Received 9 December 1997; accepted 23 March 1999.

differences in fruit production, and by trees that produce fruit in small quantities or in widely scattered individuals, fruit distribution tends to be spatially and temporally patchy (Frankie et al., 1974; Van Schaik et al., 1993). Moreover, not all fruits in a crown are ripe at any given time, and young fruits (as well as some ripe) are often laden with secondary metabolites to protect seeds (Waterman, 1984; Cipollini and Levey, 1997). Fruit-eating primates must contend with these limitations in the quality and availability of fruit resources, and are often highly selective in their fruit choices (Leighton, 1993; Ungar, 1995), using some behavioral or cognitive means to assess fluctuations in fruit availability (Garber and Paciulli, 1997), and when fruit is scarce, switch resources altogether (e.g., Rudran, 1978).

Once primates have located and acquired fruit, they are next confronted with the challenge of what to do with seeds. Seeds are the ripened ovule of a plant, essentially the plant embryo and its food supply, and are distinct nutritionally from fruit pulp. The protective coat that surrounds the seed is typically high in structural polysaccharides, and the seeds themselves are often laden with secondary metabolites (Janzen, 1971; Fenner, 1992; Chivers, 1994; Waterman and Kool, 1994). However, since parent plants may store food for the seedling in the form of cotyledons and/or endosperm within the seed, seeds can also be an excellent source of protein and fats. As such, several primate taxa, including the Pitheciinae and the Colobinae, have evolved dental and gastrointestinal features to overcome the challenges of a seed diet and exploit seeds for their nutritional content (McKey, 1978; Kinzey and Norconk, 1990, 1993; Davies, 1991). Yet, masticating and *digesting* seeds (as in the case of seed predators) and consuming fruit and *discarding* seeds are two entirely different phenomena; in the former, seeds are the desired food, while in the latter, pulp is the desired food item and seeds are an unwanted mass that must be contended with. Each feeding pattern is associated with its own set of mechanical, nutritional, and digestive challenges. In this analysis, my focus is on the phenomenon of frugivory (pulp consumption), rather than that of seed eating.

The seeds of tropical fruits range in size from less than 1 mm in length to large palm nuts that can be greater than 30 cm in width (Howe and Westley, 1988; Whitmore, 1990). In fact, seeds can account for more than half of the weight of fruits consumed by primates (Van Roosmalen, 1984; Garber, 1986). Swallowed seeds can thus represent a significant cost to a fruit eater (but not to a seed *predator*) in that they not only increase an animal's body mass, but may also displace more readily processed, nutritious digesta from the gut (Snow and Snow, 1988; Fleming, 1988; Corlett and Lucas, 1990; Levey and Grajal, 1991; Leighton, 1993; Levey and Karasov, 1994). The seeds of fruits are thereby an unwanted mass, and the adhesive pulp must be removed and seeds discarded in some way.

Along these lines, Corlett and Lucas (1990) categorized primates as being "seed swallowers," "seed spitters," or "seed destroyers," and emphasized that primates must deal with seeds in some way to make a good meal out of fruit. But no primate is purely a seed swallower or seed spitter; indeed, most primates employ some combination of these seed-handling techniques, depending on species, sex and age of the animal, habitat, fruit species consumed, and/or season (Gautier-Hion, 1980; Chapman, 1988; Corlett and Lucas, 1990; Rowell and Mitchell, 1991; Ungar, 1994; Kaplin and Moermond, 1998; Norconk et al., 1998). It is as a result of these seed-discarding behaviors that primates are increasingly recognized for their services as seed dispersers (e.g., Garber, 1986; Chapman, 1989; Tutin et al., 1991; Wrangham et al., 1994; Julliot, 1996; Lambert and Garber, 1998). Seed dispersal is a mutualistic interaction in which plants rely on animals to remove their viable offspring (seeds) away from the parent (Howe and Westley, 1988). Parent plants benefit from having their seeds removed because in this fashion, intraspecific competition among seeds and seedlings for spatially restricted resources (e.g., light, water, nutrients) may be reduced (Stiles, 1989). In addition, since host-specific pathogens and seed predators are more likely to detect seeds and seedlings

near the parent tree (Augspurger, 1983), it has been hypothesized (e.g., Janzen, 1970; Connell, 1971) that seeds and seedlings experience reduced mortality as their distance from the parent tree increases. Thus, "quality" (sensu Schupp, 1993) of dispersal has been defined by the *distance* a disperser moves the seed from the parent tree and the *density* of conspecifics with which that seed must compete for resources and avoid predator detection (Lambert, 1997).

With very few exceptions (i.e., Corlett and Lucas, 1990; Rowell and Mitchell, 1991), the influence of primate fruit-processing strategies on seed dispersal services has not been investigated to date. Yet, how a primate deals with the various constraints associated with a fruit diet, particularly those of pulp removal and seed handling, can have a major influence on both the distance of dispersal and the density of seeds dispersed. It is thus of interest to primatologists, anatomists, and tropical biologists alike to document patterns of fruit-processing behavior in primates. This information can lend insight not only into the ways in which primates deal with constraints in feeding on a patchily distributed resource that is often encumbered with large seeds and other mechanical difficulties, but also into building a predictive model regarding the seed dispersal services provided by primates to their fruiting resources.

In this paper, I investigate how chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*) in the Kibale National Park, Uganda, deal with the challenges of fruit pulp removal and seed handling in their frugivorous diet. My goals in this research were threefold: 1) to document fruit-processing behaviors in these two species, 2) to identify the factors that may shape these behaviors, and 3) to evaluate how these behaviors influence seed deposition patterns. Redtail monkeys and chimpanzees were chosen as the subject species because they are the smallest and largest anthropoids, respectively, in the Kibale forest, and moreover are representatives of two major Old World primate taxa: the great apes and the Cercopithecinae. Both body size and phylogenetic history have been argued to be strong predictors of primate feeding behavior (Schoener, 1971; Gaulin, 1979; Sailer et al., 1985). Thus, an ultimate goal of this analysis is to evaluate the extent to which differences in redtail monkey and chimpanzee fruit processing can explain broader differences in hominoid and cercopithecine fruit processing and patterns of avoiding the cost of unwanted seed mass.

METHODS

Study site

The study was conducted at the Kanyawara study site of the Kibale National Park, Uganda (0° 13′–0° 19′ N and 30° 19′–30° 32′ E (Fig. 1). The park covers an area of 766 km^2 and is situated approximately 25 km east of the Ruwenzori Mountains on undulating terrain at an elevation that ranges from approximately 1,200–1,500 m (Rudran, 1978). The temperature of this area ranges from a daily mean minimum of 12.7°C to a daily mean maximum of 25.5°C (Struhsaker, 1975). The mean annual rainfall is approximately 1,475 mm, with two rainfall peaks in March–April and September–November (Struhsaker, 1997). About 75% of the park is composed of both primary and regenerating forest that ranges from medium-altitude moist evergreen to medium-altitude semideciduous forest; the remaining 25% is occupied by a mosaic of *Pennisetum purpureum* grassland, pine plantations (established in the 1960s), and swamps (Howard, 1991). The Kanyawara study area has a well-marked trail-grid system that extends for approximately 166 km, providing access to approximately 11 km^2 of forest (Chapman and Chapman, 1995). The forest is tall and dense, with emergents that reach heights of 45–50 m.

Fruit-processing and seed-handling observations

Data on chimpanzee and redtail monkey behavior were collected between 0730–1700 hr on approximately 15 days per month from June 1993–April 1994. The redtail group was composed of 28 individuals, including one adult male, 12–13 adult females, 10 juveniles, and 4 infants. The Kanyawara chimpanzee community is reported to be composed of 41 individuals (Chapman and

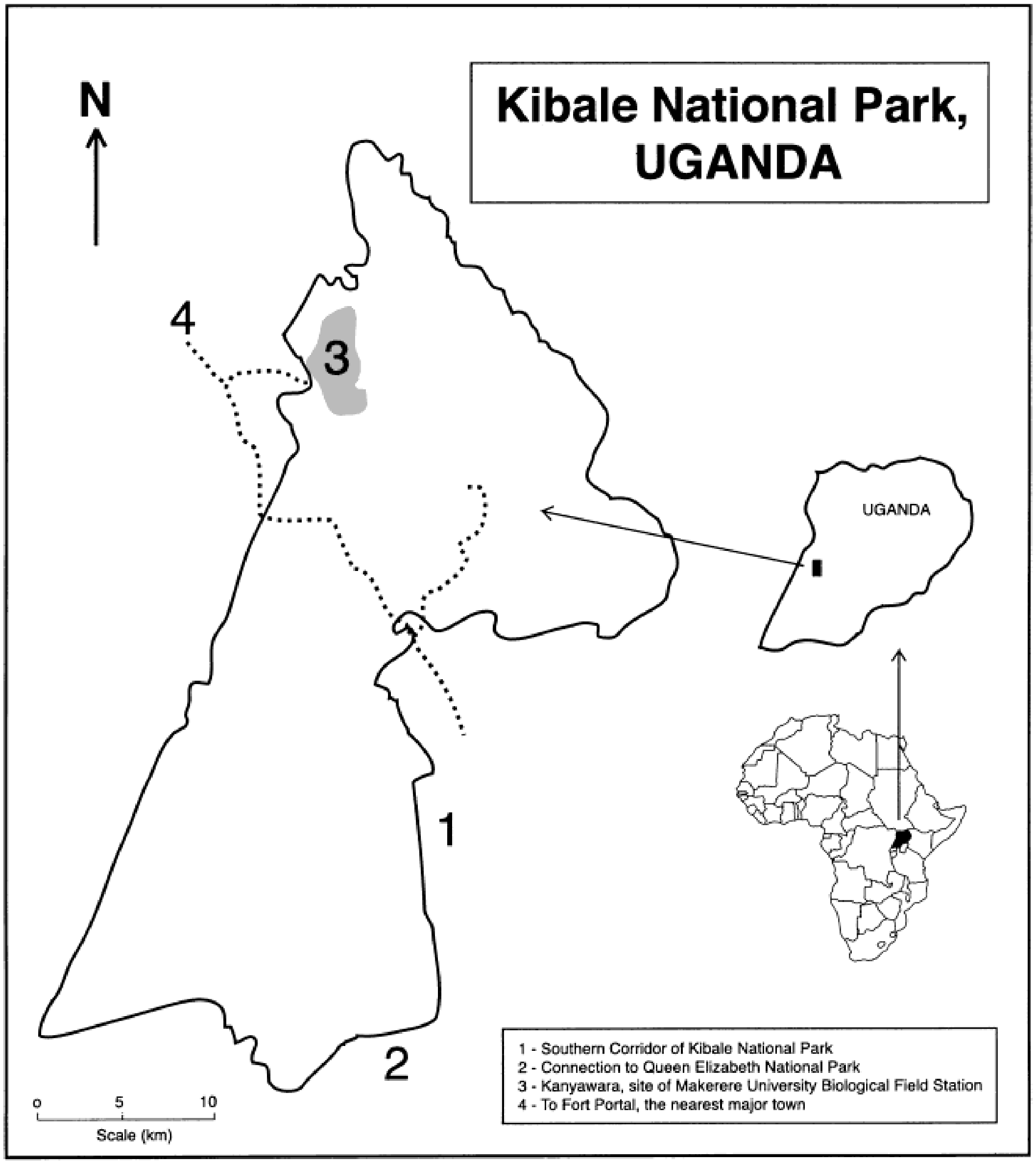

Fig. 1. Map of Kibale National Park, Uganda. Includes positioning of the park with respect to Uganda, and positioning of Uganda with respect to the rest of the African continent. Dashed lines indicate unpaved roads.

Wrangham, 1993), although I never saw all chimpanzee community members together. Rather, I observed smaller feeding parties that ranged in size from 1–13 individuals (mean Kanyawara party size = 5.11; Chapman et al., 1994).

Observations of redtail monkeys focused on a single, readily located group. Typically, the redtail monkey group was found within 30–90 min and was relatively easy to follow. On 161 days between June 1993–April 1994, I conducted group follows of the redtail monkeys, collecting data of fruit-eating regardless of the fruit species. In general, chimpanzees were located by visiting areas known to be frequented by parties and by

listening for vocalizations that travel long distances (e.g., pant hoots). On many days, chimpanzees could not be located. Even after determining their location, I would often quickly lose them again because of the swiftness with which they travel on the ground. Therefore, in addition to following chimpanzee parties (group follows), I employed a "tree follow" strategy which involved monitoring an individual tree laden with ripe fruit and waiting for chimpanzees to arrive. This method has been used effectively by several Kibale researchers (e.g., Ghiglieri, 1984; Chapman and Wrangham, 1993). Data on chimpanzee fruit-feeding were collected on 58 days.

The location of the animals within the trail system was recorded upon sighting them. For each species, an individual was chosen as a focal animal. Following Ungar (1994), data were only collected for adults or full-sized subadult animals, thereby reducing the potentially confounding behavioral variance stemming from ontogenetic differences in body size and dental morphology.

Focal animals were observed for the duration of a single fruit-eating event (FEE). An FEE was considered to begin when the focal animal removed a fruit (either manually or orally) from its attachment to the tree and ended after that fruit was handled and consumed and the seed either dropped, spat, swallowed, or destroyed. Collecting information on "fruit-eating events" allowed me to record detailed information on the fruit-processing and seed-handling behavior of the animal, as well as to use the fruit as a basic unit of measure. This method also allowed me to follow a seed through the entire course of its primary dispersal.

Fruit-eating events were quantified with respect as to whether: 1) the fruit was swallowed whole; 2) the fruit was placed into the cheek pouch (in the case of redtails) or in the lower lip (in the case of chimpanzees); 3) the pulp was removed and the seed(s) spit out or dropped, or 4) the seed was masticated and destroyed. If the seed(s) was spit out (either immediately or after being held in the cheek pouch or mouth) or dropped manually, the distance between the parent tree and where the seed was spit out or dropped was estimated ($<$1 m, 1–5 m, 5–10 m, 10–20 m, 20–50 m, 50–100 m, 100 m–1 km). Thus, frequencies of seeds that were either dropped, cheek-pouched, placed in the lower lip, spat, swallowed, or destroyed were collected, as well as where the seeds were deposited. Once the seed(s) was either destroyed, swallowed, spat, or dropped, the fruit-eating event was considered complete, and observation shifted to another member of the social group.

The criteria for selecting focal animals were based on proximity to observer and overall visibility. In the case of the redtail monkeys, where individuals were difficult to identify, this may have caused a (virtually unavoidable) bias towards some subset of more habituated group members. Although FEEs were not timed, it was clear that they varied widely in duration: from a few seconds in the case of an animal swallowing a seed, to a few minutes in the case of an animal storing a fruit in its mouth and spitting out a seed after moving. The density of vegetation, the canopy height at which the focal animals often fed, and the ease with which the primates (particularly the redtails) were alarmed, made obtaining detailed observations of fruit processing and seed handling difficult. Thus, a note about observing cheek-pouch use is warranted here. Although determining whether a seed (or fruit) has been swallowed vs. placed into the cheek pouch is difficult, it is not impossible. Most assuredly it requires good visibility; binoculars with 10$\times$ magnification and excellent optics facilitated this greatly. In addition, there are both physical and behavioral cues as to whether cheek pouches are being employed. In many cases, the skin around the external cheek visibly distends as a seed is pulled into the pouch, in which case cheek-pouch use is almost certainly occurring (indeed, in some cercopithecine species it is possible to count the approximate number of large seeds being held in the pouch!). Previous observations of captive redtails and their cheek-pouch use were useful for identifying and learning behavioral cues. For example, cheek-pouch use in redtails (and other cercopithecines) is apparent from the manner in which the mandible is maneuvered and held relative to the upper palate; the mouth is held slightly ajar,

and the mandible is rotated laterally as food is moved between the oral cavity and the pouch. Another excellent cue for distinguishing cheek-pouch use from swallowing comes from the movement of the thyroid cartilage when a seed is gulped down. When a seed is swallowed, the head is often moved back slightly, and mandibular movement ceases. Determining whether the spat seed comes from a particular fruit just removed from a tree (rather than one that was previously cheek-pouched) is more difficult and was determined from information such as the overall feeding bout (e.g., if the animal is consuming primarily leaves, but only a few fruit from a single tree, then the parent tree identity is fairly obvious). In addition, seeds were often quickly spat out after feeding on a fruit, in which case it was obvious that a seed came from the tree crown that the focal animal had just departed or was continuing to feed in.

To eliminate potential biases in the data resulting from limited visibility, data were recorded and included in the analysis *only* if the entire FEE (i.e., beginning with removal of fruit and ending with destroying, spitting, dropping, or swallowing) was observed under *high-quality* viewing conditions (the proportion of interrupted FEEs was estimated at approximately 50%). The fruit-eating results presented in this paper are not offered as an exhaustive annual diet of chimpanzees and redtail monkeys in Kibale. Although all frugivory was observed, because of the constraints of collecting detailed fruit-processing observations, data were most readily collected on a subset of tree species: these were: *Uvariopsis congensis, Pseudospondias microcarpa, Celtis durandii, Linociera johnsonii, Aphania senegalensis, Monodora myristica,* and *Cordia abyssinica*. Many individuals of these seven tree species fruited during the study period, had large fruit crops, were fed upon heavily by the two primate species, and had seeds that were readily identified in dung (Table 1). Although general patterns of fruit-eating behavior will be described in this paper, the treatment and dispersal of seeds from these seven plant species will be evaluated in detail.

Ranging and tree use

Patterns of ranging and tree use were determined in two ways. At both the initiation and conclusion of a FEE, I noted the tree species in which the focal animal was feeding. If the animal moved, distance was recorded, as well as whether the primate moved within the same tree, moved to another tree of the same species, or moved to another tree species. In addition, the location of the focal group with respect to the Kanyawara trail system (essentially, a 50-m grid) was recorded at half-hour intervals throughout the course of the day to map daily travel.

To determine whether redtail monkeys and chimpanzees deposit seeds in specific habitat types, I recorded the microhabitat into which seeds were dropped, spit, or defecated. For the purposes of this study, "microhabitat" was a 2-m area in all directions (except underneath) around a seed; this served as a broad measure of the forest structure and light regime of the dispersal microhabitat. This 2-m area was assigned a vegetation structure type (VST) score of 1–5. In this scale, 1 = closed upper canopy with a dense, herbaceous understory; 2 = open upper canopy with an understory consisting mostly of grasses; 3 = open upper canopy with a dense, herbaceous understory containing no grass species; 4 = closed upper canopy with an open understory; and 5 = open upper canopy and an open understory, e.g., a large forest gap, trail, or road.

RESULTS

Fruit-eating events

Chimpanzees and redtails were observed directly for a total of 650 contact hours between June 1993–April 1994 (chimpanzees, 225 hr; redtail monkeys, 425 hr). Data were collected on 4,001 FEEs (chimpanzees, 1,046; redtails, 2,955) on a total of 39 species of fruit (Table 2). Redtail monkey FEE observations were collected on 36 species of fruit; for chimpanzees, detailed FEE observations were collected on 20 species of fruit.

In a majority of the FEEs, the chimpanzees were seed swallowers. Seventy-seven percent of the total FEEs recorded for chimpanzees resulted in a seed being swallowed

TABLE 1. Characteristics of fruits and seeds of tree species commonly consumed by chimpanzees and redtail monkeys[1]

Fruit species	Months with fruit	DBH (cm) (n = 6)	Crown diameter	Fruit length	Fruit width	Seed length	Seed width	Number of seeds/fruit
Uvariopsis congensis	May–September	22.9 (19.3–26)	5.79	2.4 (2.27–3.52)	1.9 (1.7–2.1)	1.31 (1.1–1.8)	0.83 (0.73–0.98)	5.9 (3–8)
Celtis durandii	August–October	34.7 (17.5–45.5)	8.25	0.52 (0.39–0.53)	0.48 (0.41–0.51)	0.45 (0.39–0.51)	0.39 (0.31–0.41)	1.0
Cordia abyssinica	September–November	47.6 (34.5–62)	12.15	1.3 (1–1.6)	0.9 (0.7–1.1)	0.9 (0.7–1.1)	0.7 (0.6–0.9)	1.0
Monodora myristica	October–December	88.5 (69–138.8)	13.59	18.5 (13.1–24.2)	14.1 (11–16.7)	2 (1.7–2.2)	1.4 (1.1–1.5)	290.0 (n = 10) (160–341)
Aphania senegalensis	October–December	34.8 (16–53)	8.01	1.6 (1.1–1.9)	1.1 (1–1.4)	1.2 (0.9–1.6)	0.8 (0.6–1)	1.0
Linociera johnsonii	October–December	28.7 (16–39.8)	6.53	2.1 (1.7–2.5)	1.5 (1.3–1.6)	1.8 (1.4–2.1)	1.1 (1–1.4)	1.0
Pseudospondias microcarpa	August–September	104.7 (89–148.5)	12.8	2.4 (2–2.7)	1.6 (1.4–1.9)	1.7 (1.1–2.2)	0.9 (0.8–1.1)	1.0

[1] DBH, diameter (cm) at breast height; crown diameter (m) measured by length of east-west axis; n = 60 for all fruit and seed measures (cm), except where noted; mean followed by range (in parentheses).

TABLE 2. List of fruit species consumed by redtail monkeys and chimpanzees in Kibale National Park, Uganda, 1993–1994[1]

Fruit species	Seed-handling behavior: *P. troglodytes*	Seed-handling behavior: *C. ascanius*
Anacardiaceae		
Pseudospondias microcarpa (A. Rich.)	Swallow/spit	Spit
Annonaceae		
Uvariopsis congensis Robyns and Chesquiere	Swallow/spit	Spit
Monodora myristica (Gaertn.) Dunal	Swallow/spit	Spit
Uvaria angolensis Oliv.	Swallow/spit	
Apocynaceae		
Funtumia africana (Benth.) Stapf		Destroy
Araliaceae		
Polyscias fulva (Hiern) Harms		Spit
Balanitaceae		
Balanites wilsoniana Dawe and Sprague		Destroy
Bignoniaceae		
Markhamia platycalyx (Bak.) Sprague		Spit
Borginaceae		
Cordia abyssinica Lam.	Swallow	Spit
Ebenaceae		
Diospyros abyssinica (Hiern) F. White		Spit
Euphorbiaceae		
Neoboutonia macrocalyx Muell. Arg.		Spit/destroy
Flacourtiaceae		
Dovyalis macrocalyx (A. Rich.) Warb	Swallow/spit	
Guttiferae		
Symphonia globulifera Linn. f.		Destroy
Loganiceae		
Strychnos mitis S. Moore		Spit
Mimusoideae		
Newtonia buchanani (Baker) Gilb. and Bout.		Destroy
Moraceae		
Bosqueia phoberos Baill.		Spit
Ficus brachylepis Welw. ex Hiern	Swallow/wadge	Swallow
Ficus exasperata Vahl	Swallow/wadge	Swallow
Ficus natalensis Hochst.	Swallow/wadge	Swallow
Ficus congenesis Engl.	Swallow/wadge	Swallow
Oleaceae		
Linociera johnsonii Bak.	Swallow	Spit
Olea welwitschii (Knobl.) Gig and Schellenb.		Spit
Strombosia scheffleri Engl.		Destroy

(*continued*)

TABLE 2. *(continued)*

Fruit species	Seed-handling behavior: *P. troglodytes*	Seed-handling behavior: *C. ascanius*
Rosaceae		
Prunus africana (Hook. f) Kalkman		Spit/swallow
Rubiaceae		
Vangueria apiculata K. Schum.	Swallow	Destroy
Rutaceae		
Teclea nobilis Del.	Swallow	Spit
Fagaropsis angolensis (Engl.) Dale		Spit
Sapindaceae		
Pancovia turbinata Radlk.		Spit
Sapotaceae		
Aphania senegalensis (Juss ex Bernh.)	Swallow	Spit
Mimusops bagshawei S. Moore	Swallow	Spit
Chrysophyllum gorungosaneum Engl.	Swallow	Spit
Chrysophyllum albidum G. Don		Destroy
Sterculiaceae		
Dombeya mukole Sprague		Spit
Leptonychia mildbraedii Engl.		Spit
Ulmaceae		
Celtis durandii Engl.	Swallow	Spit/swallow
Celtis mildbraedii Engl.		Spit
Celtis africana Burm. f.		Spit
Chaetacme aristata Planch.	Swallow	Spit
Zingiberaceae		
Aframomum sp.	Swallow	
Unknown		
Unknown climber sp.		Destroy

[1] Plant nomenclature following Hamilton (1981). Seed-handling categories: Spit, pulp removed, either partially or completely, and seed spit out; Swallow, seed swallowed, apparently unharmed; Destroy, seed broken open purposely to consume endosperm or during the process of consuming fruit pulp; Spit/swallow or Swallow/spit, ingestion patterns in which some seeds of a species are spat out, while others are swallowed; includes the variation observed within the course of a feeding bout on a fruiting species as well as the variation observed over the course of a particular species' fruiting phenology; order indicates the predominant pattern; Swallow/wadge, in the case of chimpanzees, when fruit is wadged, some seeds are swallowed while others are spat out with wadge.

(i.e., of a total of 1,046 FEEs, 805 were swallows), and they swallowed seeds more frequently than did redtail monkeys ($\chi^2 = 691.32$; $P < 0.0001$; df = 1) (Fig. 2). In 97 of the 241 FEEs in which chimpanzees spat out seeds, the seeds were held in the mouth and spat out after the chimpanzee either moved in a tree (55.3%) or traveled to another tree (44.7%).

In most of the fruit-eating events, redtail monkeys were seed spitters. They spat seeds more often than did chimpanzees ($\chi^2 = 642.015$; df = 1; $P < 0.0001$), and were observed to spit seeds in 1,791 of a total 2,955 FEEs (61%). In 71% of the 1,791 FEEs in which redtails spat out seeds, fruit was placed into the cheek pouch and the seed not eliminated from the mouth until after the monkey had moved within the tree (79.8%) or to another tree (20.2%). Redtails swallowed seeds in 29.5% of the total redtail FEEs, although almost all swallowed seeds were very small in size (1–4 mm). They were observed to either consume or destroy seeds in 9.5% of the total FEEs. Chimpanzees were never observed to destroy seeds of any species.

In addition to overall patterns of seed-handling differences between chimpanzees and redtails, there was intraspecific variation in the primates' treatment of a particular fruit species. Redtails, for example, occasionally swallowed the seeds of *A. senegalensis* (1.6%; 2/129 FEEs), *C. durandii* (12.6%; 35/278 FEEs), and *P. microcarpa* (1.5%; 3/204) (Fig. 3). Chimpanzees alternated seed-handling behaviors in *U. congensis* (81% spit = 152/188; 19% swallowed = 36/188), *P. microcarpa* (6.1% spit = 4/166; 93.9% swallowed = 162/166), *C. abyssinica* (22.7% spit = 17/75; 77.3% swallowed = 58/75), *L. johnsonii* (8.9% spit = 15/168; 91.1% swallowed = 153/168), and *M. myristica* (23.2% spit = 23/99; 76.8% swallowed = 76/99) (Fig. 3). As discussed later, in large part this intraspecific variation is attributable to varying levels of fruit ripeness.

Chimpanzees and redtail monkeys removed and consumed fruits at different rates. Of fruit species exploited by both primate species, chimpanzees placed more fruit into the mouth over the course of a minute than did redtail monkeys (t = 3.93; $P = 0.04$; redtail mean = 1.57, SD = 0.47; chimpanzee mean = 4.66, SD = 2.17) (Table 3). There was no sign of a relationship between mean fruit length and mean feeding rate in either redtails (Spearman rank, 0.2029; $P = 0.7$) or chimpanzees (Spearman rank, −0.1160; $P = 0.82$).

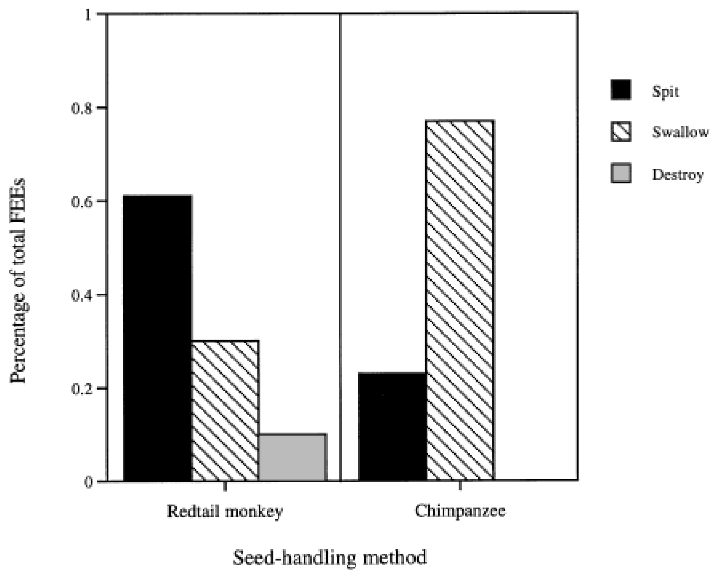

Fig. 2. Percentage of seed spit, swallow, and destroy as observed in total chimpanzee and redtail monkey fruit-eating events (FEEs). Observations from the Kanyawara study site, Kibale National Park, Uganda, June 1993–April 1994.

Qualitative description of fruit processing and seed handling

Chimpanzees and redtail monkeys exhibited differential patterns of oral fruit processing. Overall, redtail monkeys exhibited a pattern of *fine oral processing,* with heavy reliance on seed spitting and on using both anterior dentition and cheek teeth; cheek-pouch use was common. In contrast, the chimpanzees exhibited a more *coarse oral processing;* fruits were eaten rapidly, typically swallowed whole with seeds, and with less dental processing.

In general, redtail monkeys nipped off (sensu Ungar, 1994) fruit pulp with the incisors, spat out seed(s), and then further masticated the pulp using the molars (these general patterns corroborate observations on Asian cercopithecines; Lucas, 1994; Ungar, 1994). For smaller fruit species, once in the mouth, fruit was often placed into the redtail's cheek pouch (71% of the FEEs in which seeds were spit out). With larger fruits, the redtails sometimes grabbed and held the fruit in the hands as they used their incisors to nip off pulp; the seeds were then discarded manually (e.g., *P. microcarpa, L. johnsonii*). A more common pattern, however, was for the redtails to place the entire fruit into the mouth, and then manipulate it to the cheek teeth to thoroughly remove pulp (e.g., *Strychnos mitis, C. durandii*). In these cases, the fruit and seed were often placed into the cheek pouch prior to dental manipulation. Redtails also occasionally removed a fruit from the mouth, visually inspected it and then either placed the fruit back into the mouth for further processing, or dropped it to the forest floor. On occasion, the redtails used a combination of holding fruit with their hands and nipping at the fruit pulp, and then placing it into the mouth, perhaps after it had been reduced to a more manageable size, or perhaps because it required further processing with premolars and molars. Whether spat out immediately or after transport, redtails always spat out seeds singly, while chimpanzees often spat out a number of seeds simultaneously.

Fruit consumption by chimpanzees was rapid, and they often placed more than one fruit into the mouth at a time. For example, focal chimpanzees were observed to place anywhere from 1–6 *U. congensis* fruits into the mouth simultaneously. The fruits were then often manipulated against the lower incisors as fruit pulp and juices were separated from the seeds. Likewise, *F. exasperata* fruits were shoveled into the mouth in bunches of five or more in rapid sequence, followed by a break during which time the seeds and pulp were processed in the lower

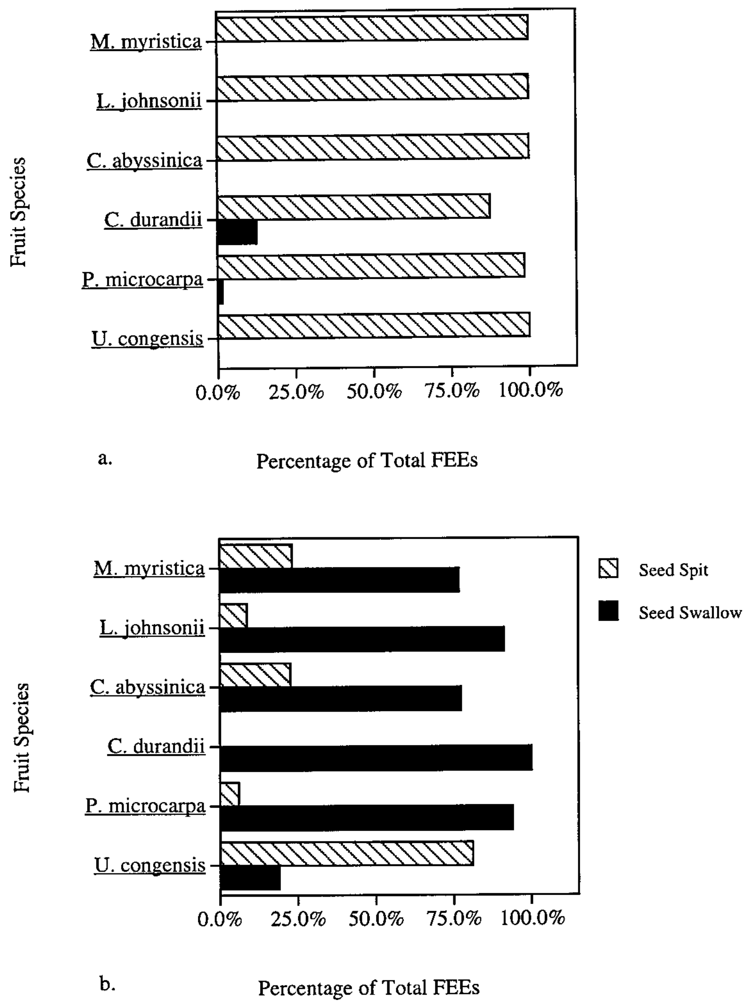

Fig. 3. Percentage of spit vs. swallow fruit-eating events (FEEs) for seven most commonly consumed fruit species. **a:** Observations of redtail monkeys. **b:** Observations of chimpanzees.

TABLE 3. Feeding rates in chimpanzees and redtail monkeys[1]

Fruit species	Chimpanzee	Redtail monkey
Celtis durandii	Mean = 7.9, n = 10, SD = 1.73	Mean = 2.22, n = 30, SD = 0.46
Uvariopsis congensis	Mean = 4.1, n = 30, SD = 0.66	Mean = 1.1, n = 30, SD = 0.78
Pseudospondias microcarpa	Mean = 5.7, n = 30; SD = 0.89	Mean = 1.9, n = 30, SD = 0.54
Cordia abyssinica	Mean = 2.9, n = 5, SD = 0.56	Mean = 1.4, n = 5, SD = 0.1
Aphania senegalensis	Mean = 2.7, n = 30, SD = 0.56	Mean = 1.23, n = 30, SD = 0.43
Linociera johnsonii	Mean = 1.3, n = 30, SD = 0.36	Mean = 1.3, n = 30, SD = 0.33

[1] Feeding rates, number of fruits placed into mouth/min; SD, standard deviation.

lip. Chimpanzees were rarely seen to use teeth other than their anterior dentition. After removing fruit from a branch (primarily with the hands, although sometimes directly with the mouth), chimpanzees often maneuvered the fruit with their muscular lips against the anterior dentition, resulting in a "wadge" (Goodall, 1986) of fruit pulp, skin, and fiber which was often left in the lips for several minutes. In this manner, fruit juices were apparently extracted by sucking at the pulp for up to several minutes (duration was not quantified), and the seeds eventually spat out. Wadging was observed

for several fruit species, but this pattern was particularly common when consuming ripe figs (although figs *can* be swallowed whole, particularly when not completely ripe). When wadged, some fig seeds are swallowed, but typically the mass of fruit and seeds is eventually spit out. Canines were occasionally used when exploiting fruits that were difficult to open and consume. For example, when feeding upon the very hard and large (mean width, 14.1 cm) *Monodora myristica* fruit, the chimpanzee would stabilize the fruit with its hands and then smash open the fruit against a hard branch, finishing the job with the canines. In general, once the chimpanzees began to consume fruit, feeding was intense, often lasting up to several hours in a single tree (e.g., *P. microcarpa*) or stand of trees (e.g., *U. congensis*).

In some cases the redtails and chimpanzees exhibited variable ingestive behaviors when feeding on the same fruit species; i.e., they sometimes swallowed the fruit and seed of a species whole, while on other occasions they spat out or wadged the seeds of this same fruit species. Differences in fruit/seed treatment appear to be related to the relative ripeness of the fruit. For example, in 12% of the FEEs for *Strychnos mitis*, redtails fed on unripe fruit (in July and August) and in these cases swallowed the fruit whole. When *S. mitis* fruit was ripe (in September and October), the seed was always spit out. Likewise, 13% of *C. durandii* fruits were swallowed whole by the redtails; these swallows also occurred when the fruit was unripe. Similarly, although chimpanzees prefer ripe fruit in general, they will sometimes swallow unripe figs whole, but wadge figs and spit out seeds when ripe. In general, it seems likely that when fruit is unripe, primates must swallow fruit in order to extract difficult-to-remove green pulp from seeds.

Ranging behavior

Full-day observations indicated that redtail monkeys traveled an average of 1,178 m (SD, 399.8) in a day (minimum, 700 m; maximum, 2,500 m; n = 26 days) (Fig. 4). The position of a group was mapped out on a 100 × 100 m grid, and in a 10-month period (June 1993–April 1994), the focal redtail group used a total area of 49 ha. Fifty percent of the time the redtails used 35% of their total area, approximately 17 hectapes (ha). When calculating range area, both partial and full days were used.

Chimpanzees ranged widely in a day, often moving from one large fruiting tree to another and feeding along the way on terrestrial herbaceous vegetation (THV). Determining total day range for the chimpanzees proved to be extremely difficult. Once the chimpanzees decided to travel, they did so at an extremely fast pace, often eluding my attempts to follow. On several occasions, however, I followed all male parties for approximately 3 km. This is consistent with chimpanzee day ranges reported elsewhere (e.g., Gombe, mean female day range, 3 km; mean male day range, 4.3 km; Goodall, 1986). Although I was unable to produce an estimate of total area used by Kanyawara chimpanzees, recent work suggests that between 1989–1992, the Kanyawara chimpanzee community used an area of 2,220 ha (extrapolated from Chapman and Wrangham, 1993).

Both chimpanzees and redtail monkeys were most commonly found consuming fruit in areas with a closed upper canopy and a dense, herbaceous understory (VST1) (chimpanzees, 44%; redtails, 52%). The redtail monkeys and chimpanzees were never seen to eat fruit in areas with a closed upper canopy and an open understory or an open upper canopy with an open understory (VST1 and VST2). The fact that these two species were not seen to feed in these areas probably reflects the habitat of Kanyawara in general (i.e., there is relatively little unvegetated forest floor; personal observation), and also that it is unlikely that these primates would consume fruit in completely nonforested and open areas. Chimpanzees may travel through such areas, en route to other fruiting trees, but fruit-feeding in large gaps is unlikely because of a paucity of large fruiting trees in such areas (Wrangham et al., 1994).

Seed-dispersal distance

Although chimpanzees spat out seeds in only 240/1,046 of the total chimpanzee FEEs, when both chimpanzees and redtails spat out the seeds of a particular species, they

Fig. 4. Home range of focal redtail monkey group in the Kanyawara study site, Kibale National Park, Uganda. Range extrapolated from data collected between June 1993–April 1994. Larger polygon refers to area used in a total of 95% of observations. Smaller polygon refers to area used in 50% of observations (core area).

deposited seeds in different patterns with respect to proximity of the parent tree. In those cases in which individuals moved before spitting, chimpanzees traveled to a tree of the same species 90% of the time, while redtails traveled to a tree of the same species 83% of the time.

The spitting distance data were organized into distance categories. In 67.4% of the 239 FEEs in which chimpanzees did not swallow seeds, they moved less than 1 m before spitting out seeds, while redtails moved less than 1 m in 49.3% of the FEEs (993/2,014; $\chi^2 = 52.29$; P 0.0001; df = 1). There was no difference in frequency of movement in the 1–5-m interval (chimpanzee, 57/239; redtail, 487/2,012; $\chi^2 = 0.0128$; $P = 0.9$; df = 1). Redtails moved seeds significantly more often in the greater distance categories than chimpanzees, including 5–10 m ($\chi^2 = 10.85$; $P < 0.001$; df = 1) and 10–20 m ($\chi^2 = 18.470$; $P < 0.0001$; df = 1).

In Figure 5, I have graphed simultaneous confidence intervals for multinomial probabilities based on cell frequencies (Bailey, 1980). The confidence intervals indicate the probability of the frequencies being distributed around the observed value rather than the mean, and are generated on the probabilities of the observed frequencies occurring in the proportions seen in Figure 5. As this is a distribution of multinomial probabilities, a change in the proportion in any one category will influence the proportion in all other categories. Results indicate that redtails and chimpanzees differ in their pattern of seed-spitting with regard to proximity to the parent tree. More specifically, on those occasions when chimpanzees do spit out seeds, they do so significantly more often

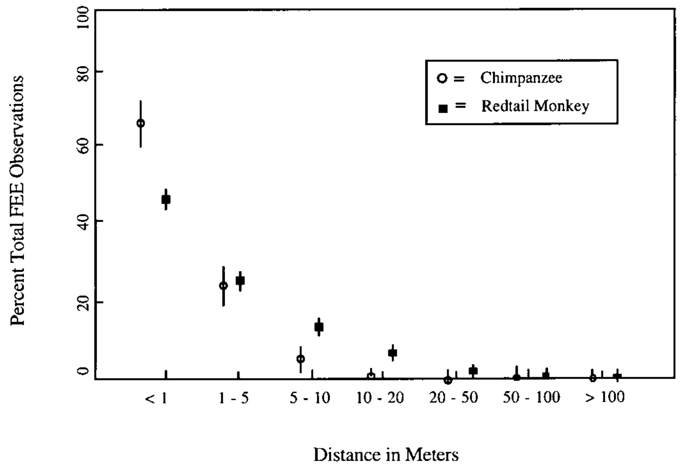

Fig. 5. Multinomial confidence intervals for spitting distance categories (procedure following Bailey, 1980). Extrapolated from chimpanzee and redtail monkey fruit-eating event (FEE) data.

within 1 m of the parent tree than do the redtails, which influences the proportions of chimpanzee seed-spitting in other distance categories (i.e., greater from the parent tree).

There were some differences in the distances at which chimpanzees and redtails spat seeds. For example, redtails spat seeds underneath the crown of *U. congensis* (average crown length, 5.8 m) in 113 of 182 FEEs (62%) (Fig. 6), while chimpanzees spat these seeds under parents in 165 of 185 FEEs (89%) $\chi^2 = 3.35$; df = 1; $P \leq 0.001$). No differences were found for other tree species. For *M. myristica,* redtails spat or dropped seeds underneath the parent tree's crown (average crown = 13.6 m) in 23 out of 24 FEEs (96%), while chimpanzees spat these seeds under the crown in 152 of 158 FEEs (96%) ($\chi^2 = 0.635$; df = 1; NS) (Fig. 6). Chimpanzees spat *C. abyssinica* seeds under the parent's crown in 14 of 17 FEEs (82%), and redtails spat out seeds in 100 of 107 *C. abyssinica* FEEs (93%) ($\chi^2 = 0.139$; df = 1; NS) (Fig. 6). Of the other four study species in which redtails (but not chimpanzees) were observed to commonly spit seeds (i.e., *P. microcarpa, A. senegalensis, C. durandii,* and *L. johnsonii*), they spat them under the crown of these species in 83.8% of the total FEEs (759) for these four species (Fig. 7).

In terms of seed deposition, the trends toward using certain vegetation structure types mirrored the fruit-consumption patterns. For example, the animals never spat seeds of the seven study species into VST categories 4 or 5. Of a total 1,143 seed-spitting events, redtails spat seeds into VST1 in 52% of the total FEEs. Redtails spat seeds into an area of open upper canopy with an understory consisting mostly of grasses (VST2) in 23% of the total FEEs and into an area of open upper canopy with a dense, herbaceous understory containing no grass species (VST3) in 25% of the FEEs. Chimpanzees were observed to spit seeds into VST1 in 44% of the total (537) FEEs, into VST2 in 39% of the total FEEs, and into VST3 in 17% of the total FEEs. Vegetation structure types were recorded for both the microhabitat type in which the fruit was removed ("before") and the habitat type into which the seed was deposited ("after"). Redtails significantly more often switched VST when spitting out seeds than chimpanzees ($\chi^2 = 31.04$; df = 1; $P = 0.037$), although the numbers were very minor (redtail "before" vs. "after" VST differed by only 4.8%; chimpanzee "before" vs. "after" VST differed by 3.2%).

While species of seeds found in dung could typically be identified, it was virtually impossible to determine the identity of the parents of seeds found in that dung. Moreover, the sample of dung containing seeds of the seven focal tree species was quite small. Nonetheless, some potentially interesting patterns emerged in terms of defecation of seeds and their relative proximity to adult trees of that

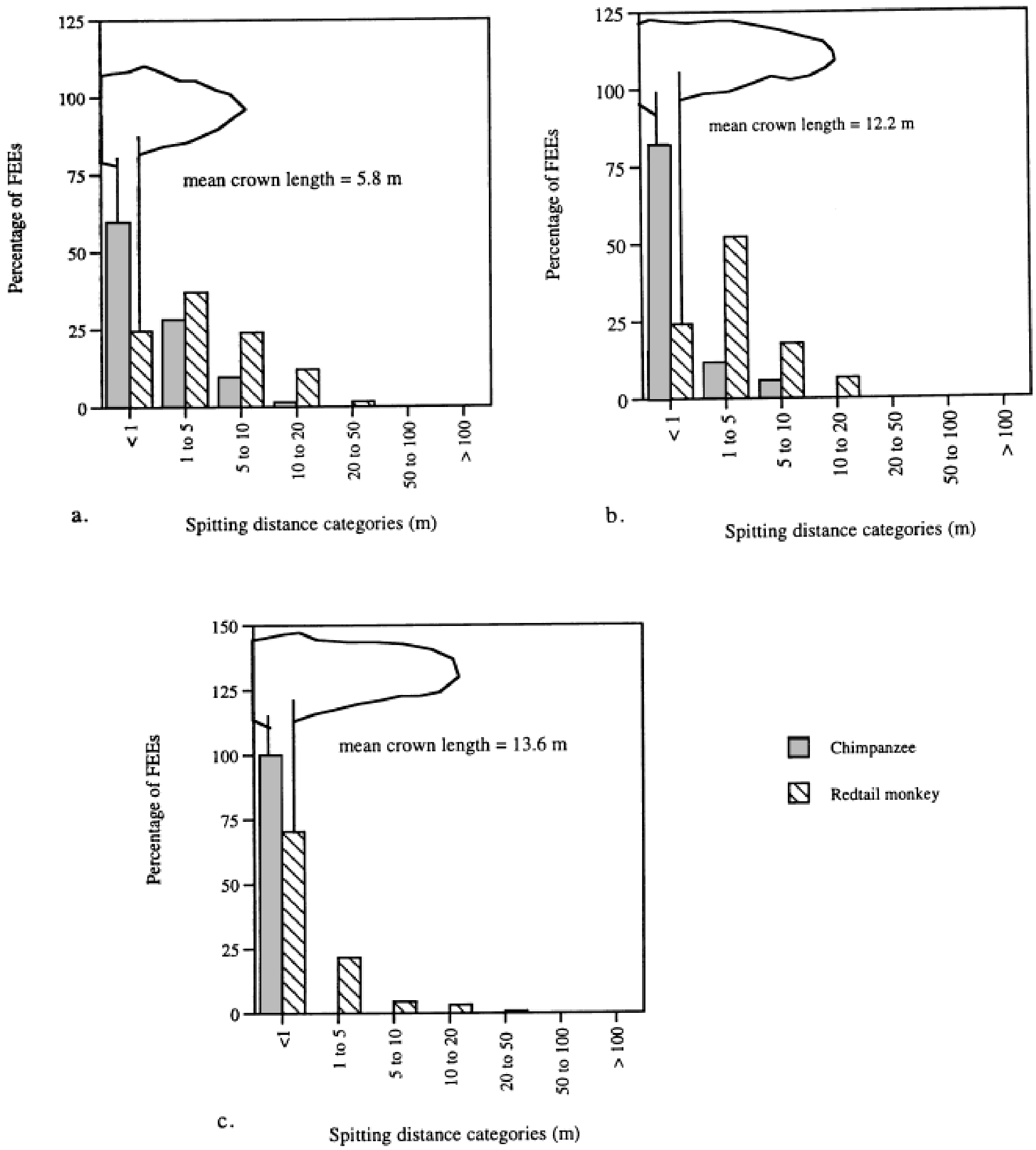

Fig. 6. Percentage of spit seeds deposited by redtail monkeys and chimpanzees. Spitting distance categories represent the distance seeds were removed away from crowns of adult trees, and not the bole. **a:** Percentage of spit seeds in total number of *Uvariopsis congensis* FEEs. **b:** Percentage of spit seeds in total number of *Cordia abyssinica* FEEs. **c:** Percentage of spit seeds in total number of *Monodora myristica* FEEs.

same species. For example, 25% of chimpanzee dung samples (21/81) were found under the crowns of tree species represented by seeds in the dung sample (e.g., of 24 dung samples containing *P. microcarpa* seeds, 18 were found under fruiting *P. microcarpa* trees). Of redtail dung containing seeds, only 0.03% (4/135) were found under tree species represented by seeds in the dung ($\chi^2 = 29.09$; $P < 0.001$; df $= 1$).

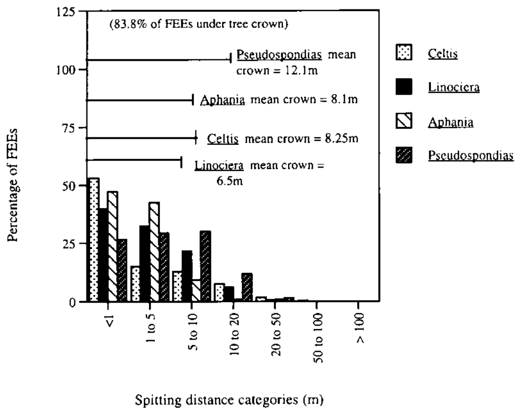

Fig. 7. Percentage of spit seeds deposited by redtail monkeys under crowns of adult *Pseudospondias microcarpa, Aphania senegalensis, Celtis durandii,* and *Linociera johnsonii.*

Seed-dispersal density

When redtail monkeys spat seeds, they spat them out singly as fruit were processed, while chimpanzees typically spat out seeds in wadges. There also were differences in seed clump density when seeds were swallowed. Swallowed seeds were deposited in dung in seed clusters of varying densities under the parent tree or elsewhere in the forest. Fifty-five percent of redtail dung samples ($n = 135$) contained seeds, but most of these seeds (84%) were *Ficus* spp. and very small (1–2 mm in size); only 0.08% of dung samples had seeds greater than 0.5 cm. The number of large seeds found in a single redtail dung ranged from 1–6 (mean, 3.5). No redtail dung samples contained more than one species of large seed.

All chimpanzee dung samples ($n = 81$) contained seeds. Ninety-three percent of these samples contained seeds >0.5 cm in length. The number of large seeds found in a single chimpanzee dung sample ranged from 1–149 (mean, 37), and 11% (9/81 samples) contained at least two species of large seeds.

An estimation of overall numbers of fruits removed by chimpanzees and redtail monkeys can be extrapolated. Redtails feed on fruit at an average rate of 1.6 fruits/min, and chimpanzees consume fruit at an average rate of 4.7 fruit/min. Although there is large seasonal and daily variance, on average redtails and chimps feed on fruit for approximately 2 hr/day. This means that an individual redtail could remove approximately 188 fruits/day, and a chimpanzee 559/day. In Kibale, redtails occur at a density of 130 individuals/km^2, while chimpanzees occur at a density of 2.5 individuals/km^2 (Wrangham et al., 1994). Thus, in a single day, the individuals in the redtail monkey population could potentially remove 24,492 fruits/km^2, and chimpanzees, 1,398/km^2.

DISCUSSION

Redtail monkeys and other cercopithecines: fine oral processing and seed spitting

Redtail monkeys spit out the majority of the seeds of fruit they consume. This is a pattern of fruit processing that has been observed in other cercopithecine species, including *Macaca fascicularis, Cercopithecus cephus, C. nictitans,* and *C. pogonius* (Gautier-Hion, 1980; Corlett and Lucas, 1990). Corlett and Lucas (1990) pointed out that cercopithecines in general can be distinguished from other anthropoids on the basis of their behavioral tendency to spit seeds. Indeed, in the scheme by Corlett and Lucas (1990) of "seed swallowers," "seed spitters," or "seed destroyers," only members of the subfamily Cercopithecinae are categorized as "seed spitters." However, while these authors argued that patterns of seed handling are the result of divergent strategies to deal with the high secondary metabolite load found in most seeds, here I suggest that factors besides (or in addition to) seed toxicity can shape different patterns of processing.

Redtail monkeys can be distinguished from chimpanzees in their fine oral processing of fruit and seed-spitting. These behaviors are facilitated by several oral features, including cheek pouches, broad central incisors, and large molars with high shearing crests. All extant species of Cercopithecinae have cheek pouches, which are bilateral, elongated sacculations found in the inferior buccinator pocket; food is moved between the pouch and the oral cavity through a slit-like opening (Murray, 1973, 1975; Fleagle, 1999). This region of the mouth is highly inner-

vated, is kept moist with amylase-rich saliva, and is lined with mucous membranes with high concentrations of mucous and seromucous glands (Jacobsen, 1970; Murray, 1975; Rahaman et al., 1975; Jones et al., 1986; Manger et al., 1995; Lucas and Corlett, 1998). This moist and sensitive environment presumably softens unripe fruits and initiates preswallowing digestion, thereby facilitating subsequent dental processing and removal of pulp from large seeds.

Removing pulp from seeds is also facilitated by the large anterior and postcanine teeth that characterize cercopithecine dentition (Lucas and Teaford, 1994). A large component of fruit-pulp removal is accomplished with the anterior dentition in many frugivorous primates (Fleagle, 1999; Lucas and Teaford, 1994; Ungar, 1994). In the data presented here, incisors were used often by the redtails in the initial nipping and removal of pulp from seeds. These observations corroborate those of Lucas and Teaford (1994, p 198) who suggest that "these animals [i.e., cercopithecines] do as much work with the front of the mouth, cleaning fruit skins, as they do inside the mouth, removing fruit flesh from the seeds. After cleaning off the fruit skin and flesh, they spit the seed out." Unlike seed swallowers (e.g., apes) who have large anterior dentition, but small postcanine teeth, cercopithecines have large postcanine teeth and bilophodont molars. Thus, after removing pulp with their broad incisors and spitting out the seed, the pulp is then processed by the relatively high-crested bilophodont molars, in preparation for swallowing (Lucas, 1994). Although cercopithecine molars have blunter lophs than colobines, a benefit of bilophodonty in general is that it results in greater shearing capacities and greater crushing surfaces than bunodont molars (Kay and Sheine, 1979). Cercopithecines can thus remove pulp from seeds and then masticate it more finely than other primates with relatively smaller, more rounded postcanine teeth (Lucas and Teaford, 1994). This process is facilitated by the fact that fruits, having been in the cheek pouches (e.g., 77% of redtail FEEs fruits were placed into cheek pouch before seeds were spat out), have already undergone some amount of amylization.

The question now becomes, *why* are redtail monkeys and other cercopithecines seed spitters? Or, in other words, why don't these monkeys swallow large seeds? Ingested seeds are costly to frugivores because they increase an animal's body mass and also displace incoming nutritious digesta (food) from the gastrointestinal tract (Snow and Snow, 1988; Fleming, 1988; Phua and Corlett, 1989; Corlett and Lucas, 1990; Levey and Grajal, 1991; Leighton, 1993; Levey and Karasov, 1994). This will be especially true for frugivores with lengthy gut retention times. As demonstrated by data stemming from gut passage trials, as well as across-species analyses, the Cercopithecinae have among the longest (both absolutely *and* relatively) gut transit times across the Primate order (Clemens and Phillips, 1980; Clemens and Maloiy, 1981; Maisels, 1993; Lambert, 1997, 1998; see Warner, 1981, for definitions of digestive passage times). Seed spitting may thus be important for cercopithecines because if large-seeded fruit were swallowed whole to remove pulp, then the energetic cost of indigestible seed ballast would be incurred for an absolutely and relatively long time. Moreover, it could severely limit space for incoming food. Many frugivores exhibit adaptations to deal with these energetic and food-limiting constraints. Frugivorous birds, for example, exhibit a wide variety of behavioral and morphological adaptations to deal with voiding seeds quickly, including crops, gizzards, large bills, seed mandibulation and regurgitation, and extremely fast gut passage rates (Sorenson, 1984; Moermond and Denslow, 1985; Snow and Snow, 1988; Levey and Grajal, 1991; Levey and Karasov, 1994; Corlett, 1998). Flying foxes (Pteropodidae) too will avoid ballast by only removing the juice of fruits and discarding remaining fiber and seeds (Phua and Corlett, 1989; Corlett, 1998). Here, I suggest that seed spitting in cercopithecines is another mechanism to avoid seed ballast.

The fact that the seeds swallowed by redtails and other cercopithecines tend to be very small supports this hypothesis. Virtu-

ally all of the seeds that were swallowed by redtail monkeys were small-seeded species, and less than 1% of the dung samples contained seeds that were larger in their longest axis than 0.5 cm. Corlett and Lucas (1990) and Lucas and Corlett (1998), using *Macaca fascicularis* as an example, suggested that cercopithecines have very low swallowing thresholds, and those seeds that are swallowed are only swallowed because they cannot be detected or because the size cannot be gauged; only seeds with a longest axis of about 3 mm were swallowed by this macaque species. In the present study, 90% of the seeds observed to be swallowed by redtails were *Ficus* spp. seeds (longest axis, 2 mm). This mirrors the dung sample results, in which 84% of the seeds found in redtail dung were *Ficus* seeds. Figs are not a true fruit, but a synconium, and each synconium can contain literally hundreds of very small seeds that are virtually impossible to separate from the pulp matrix (i.e., fig wall) (Lambert, 1989). Separating tiny seeds (1–2 mm, longest seed axis) from the fig wall would significantly increase handling time and decrease energy intake (Leighton, 1993). In addition, fig seeds are so small that they are unlikely to reflect the cost that large seeds do in terms of ballast and displacing nutritious digesta (Howe and Vande Kerckhove, 1981; Levey and Grajal, 1991; Leighton, 1993).

It should be noted that while seed spitting is the typical cercopithecine pattern of seed handling, these primates can also be seed destroyers. For example, Rowell and Mitchell (1990) reported that redtail monkeys in Kakamega destroy the seeds of *Prunus africana,* Gautier-Hion et al. (1993) found that in Botsima, Zaire, *Cercopithecus wolfi* were mainly seed predators, and in Rwanda, *Cercopithecus mitis* and *C. l'hoesti* can be seed predators depending upon overall resource availability (Kaplin and Moermond, 1998). This is not just an African trend: in Singapore, *Macaca fascicularis* destroy the seeds of approximately 10% (9/88) of the fruit species they ingest (Lucas and Corlett, 1998). In these cases, however, seeds do not represent a cost in terms of displacing nutritious digesta, but are part of the digesta itself.

Chimpanzees and other apes: coarser oral processing and seed swallowing

An alternative pattern of pulp removal is exhibited by chimpanzees, who swallow many fruits whole, including the seeds. In contrast to what was observed in redtail monkeys, seed swallowing in chimpanzees was not limited to small seeds (e.g., *Monodora myristica* seeds were regularly swallowed and recovered in dung samples, even though these seeds have a length of over 2 cm). Wrangham et al. (1994) reported similar results, and documented that Kibale chimpanzees swallow and disperse the seeds of 59 species of fruit. These seeds ranged in size from less than 1 mm (*Ficus* spp.) up to 2.7 cm (*Cordia millenii*); 53% of these species are large-seeded (i.e., length greater than 0.5 cm). Swallowing large seeds appears to be a common pattern of fruit-processing among the apes. Indeed, gibbons, bonobos, orangutans, and Western lowland gorillas are reported to commonly swallow and defecate large seeds (Chivers and Raemakers, 1986; Idani, 1986; Galdikas, 1982; Tutin et al., 1991). For example, Tutin et al. (1991) reported that gorillas in Gabon defecate intact seeds of at least 65 fruit species, 66% of which are large-seeded species (i.e., 10/65 = 1.5–4 cm; 33/65 = 0.5–1.5 cm).

Chimpanzees exhibit an overall coarser level of oral processing relative to redtail monkeys. Fruits were swallowed rapidly, with little dental processing. As in cercopithecines, the factors that shape chimpanzee fruit-processing behaviors are likely a result of interactions among oral anatomy, body size, and digestive transit times. Although chimpanzees have broad incisors, they lack the relatively large postcanine teeth, high-crested bilophodont molars, and cheek pouches that characterize cercopithecine oral anatomy (Fleagle, 1999; Lucas and Teaford, 1994). In addition, chimpanzees are large animals, exhibiting the more typical emphasis of fast (relative to body size) digestive processing common to frugivores (Milton, 1984; Milton and Demment, 1987; Levey and Grajal, 1991; Lambert, 1997). Because seeds swallowed by chimpanzees are likely to move through the gastrointestinal tract relatively faster than in the case of redtails

and other cercopithecines, they are also less likely to incur such a cost in terms of seed ballast and displacement of nutritious digesta. Moreover, being a large animal, swallowed seeds will represent a smaller mass relative to chimpanzee body size. A potential result of this is that natural selection has been less intense in hominoids than in cercopithecines for evolving behavioral mechanisms to avoid the cost of seeds in the gut. Since chimpanzees do not have the oral features that cercopithecines have to facilitate fine levels of pulp removal, they must swallow many fruits whole in order to fully extract pulp off of seeds. This scenario may help to explain why another ape, the Kloss gibbon (*Hylobates klossii*), can consume up to a kilogram of seeds in a feeding bout (Whitten, 1982).

Of course, chimpanzees are not without oral mechanisms to process fruit, and they do not always swallow seeds (i.e., 23% FEEs = seed spit). In chimpanzees and orangutans (*Pongo pygmaeus*), prehensile and muscular lips are often used in combination with anterior dentition to process fruit (Galdikas, 1982; Ungar; 1994). Walker (1979) suggested that because pongid lips are so mobile, they can be used effectively as a third appendage and, moreover, are functionally comparable to the cercopithecine cheek pouch since they serve to store food. Ungar (1994) proposed that pongid lip mobility may have evolved to facilitate rapid food ingestion. Finally, since the interior labial surface contains numerous pores associated with salivary glands (Bourne and Golarez de Bourne, 1972), processing fruit in prehensile lips may also serve to soften fruit and perhaps provide some amount of oral digestion via amylization.

Chimpanzee prehensile lips certainly facilitate “wadging” of fruit species. Wadging may be used by chimpanzees in fruit feeding when seeds in the gut have exceeded some critical point in terms of ballast and displacement of incoming food. Chimpanzees both swallow and spit out seeds of some fruit species in Kibale. This is true primarily with figs, but with other species as well. For example, chimpanzees were observed to employ both fruit spitting (via wadging) and seed swallowing when handling seeds of *U. congensis* (Fig. 3). Chimpanzees rapidly swallow *U. congensis* fruit and seeds whole at the beginning of feeding bouts, but then wadge and subsequently spit out seeds of this fruit later on in the feeding bout. Chapman (personal communication) has observed that the stomachs of chimpanzees become visibly distended during these occasions, and that chimpanzees typically only begin to spit out *U. congensis* seeds when the stomach is bloated and taut in appearance. These observations support the hypothesis that seeds can become a burdensome, indigestible mass, and that behavioral mechanisms need to be employed to minimize seed cost in terms of ballast and the inhibition of incoming food.

Implications for the dispersal of seeds

Seed spitting and seed swallowing are not only fundamentally different strategies for dealing with the constraints of pulp removal and seed ballast, but these behaviors can also significantly impact the way seeds are dispersed in a forest. Indeed, while Kibale chimpanzees and redtails are both arboreal feeders, are highly frugivorous, and share many fruit species in common, they clearly differ in terms of the *distance* to which seeds are removed, in the *density* of seed dispersal clusters, and in the total number of seeds removed. Cercopithecines are generally “seed spitters.” In the present case of redtail monkeys, this meant that seeds were spat close to the parent tree (within 10 m), and always deposited singly (a “close-single” pattern). In contrast, chimpanzees are generally “seed swallowers” and defecate seeds in large clusters that can number in the hundreds; and while they may spit seeds close to the parent tree (approximately 20% of FEEs), they are more likely to defecate them at some distance away from the parent tree (a “far-clumped” pattern).

The influence of these dispersal patterns on seed survivorship and seedling recruitment is difficult to evaluate, largely because of a paucity of data on tree species’ requirements for good dispersal. In their classic papers, Janzen (1970) and Connell (1971) proposed that movement of seeds even a short distance from parent trees significantly increases the probability of seed and seedling survival. While the predictions

stemming from these early articles were seminal in the history of seed-dispersal research (Herrera, 1986), the degree to which "seed escape" and the so-called "Janzen-Connell model" apply generally to tropical tree species and are predictable of broad patterns of seed and seedling mortality and survivorship is questionable (Howe and Smallwood, 1982; Herrera, 1986; Howe, 1989). As more data are garnered on the fate of seeds and seedlings in tropical forests, it is evident that there exists large interspecific variation in the degree to which density-dependent factors influence seed fate. For example, while many species exhibit greater survivorship away from parent trees, others fare equally well whether they are below the crown of parents or dispersed, while yet others experience the greatest levels of survivorship beneath conspecifics (Chapman and Chapman, 1996; Howe, 1977; Condit et al., 1992).

Given the range in seed survivorship patterns among tropical plant species, broad generalizations of "good" vs. "bad" primate dispersal quality are not tenable, and shed no light on the complexity of animal/plant dynamics in the tropics. Depending on the requirements of the particular seed species, primates provide a dispersal *service* or else have a neutral or deleterious effect. For example, while chimpanzees move a large number of seeds away from parent trees and have thus been argued to be important seed dispersers (Wrangham et al., 1994), they also defecate these seeds in high-density depots. For some seed species, such "clump-dispersal" (sensu Howe, 1989) can be as attractive to rodent/insect predators and fungal pathogens as the parent tree environment (Lambert, 1999), and long-distance travel may result in some seeds being carried to potentially unsuitable habitats. However, there is some evidence that when some seed species are deposited in large clumps, rodent seed-predators can become satiated and cease to consume seeds (Janzen, 1976; Crawley, 1992; Willson and Whelan, 1990). Moreover, potential costs of being dispersed in a high-density seed clump may be offset by the benefit of passing through the gastrointestinal tract. Wrangham et al. (1994), for example, found that seed passage through a chimpanzee's gut improves germination percentages as well as shortens the time to germination. These results are corroborated by other research on great apes (Takasaki, 1983; Idani, 1986). Thus, with regard to a characterization of seed-dispersal quality, chimpanzees move seeds in a "far-clumped" pattern. However, the impact of this pattern on seed survivorship will vary across tree species.

Similar assessments of cost and benefits must be weighed when evaluating cercopithecine seed dispersal. In their discussion of the importance of primates as seed dispersers in the Kibale forest, Wrangham et al. (1994) suggested that chimpanzees may be more important seed dispersers than cercopithecines, despite their lower population density. This assessment was made, however, without taking cercopithecine seed spitting into account. If it is assumed that blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Lophocebus albigena*) have similar feeding rates as the redtails, then monkeys can potentially remove up to 33,840 fruits/km^2/day in comparison to the total ape removal of 1,398 fruits/km^2/day. Furthermore, seed swallowing and defecation some distance away from parent trees are not necessarily tantamount to a seed dispersal service, but may be neutral or deleterious depending on the tree species. For example, redtails scarify the seed surface with their teeth (personal observation) and deposit the seeds singly, rather in large clumps. This may give some tree species an advantage, even though the seeds are deposited close to or beneath the parent tree's crown. Indeed, the seeds of some species clearly benefit from redtail seed spitting. For example, in the case of *Strychnos mitis*, 83% of seeds spat out by redtails germinated, while only 12% of the unprocessed fruits survived to germination (Lambert, 1995). Unprocessed fruits (with pulp remaining on the seeds) were also more likely to be attacked and damaged by seed predators and fungal pathogens. Thus, although seeds were dispersed under or near parent trees, a pattern which might be deleterious for some tropical tree species, for *S. mitis*, redtail monkey fruit processing was beneficial, at least at the seed and seedling stage.

These results and the discussion underscore the problems with generalizing the services of a disperser across tree species, and offer challenges to those interested in unraveling the complexities of plant-animal interactions. It is apparent that not all primates process and disperse seeds in similar patterns. The "close-single" dispersal pattern of redtail monkeys, and the "far-clumped" dispersal pattern of chimpanzees may be neutral, beneficial, or deleterious services, depending upon the tree species and habitat at hand. Nonetheless, gaining an understanding of why a primate handles seeds in the manner in which it does constitutes the first step in building a predictive framework regarding primate fruit-processing and seed-dispersal patterns.

ACKNOWLEDGMENTS

I thank the Office of the President, Uganda, the Uganda National Council for Science and Technology, and the Uganda Forestry Department for granting me permission to work in Uganda. I thank Gilbert Isabirye-Basuta and John Kasenene for facilitating my work and for allowing me to conduct research at the Makerere University Biological Field Station. Agaba Erimosi was invaluable in his assistance in the field. Colin and Lauren Chapman have been instrumental in my work at Kibale at all stages, and I am deeply appreciative for their support. I gratefully acknowledge Paul Garber, Colin Chapman, Carol Augspurger, Stan Ambrose, Peter Lucas, and Steve Leigh for their thoughtful comments on earlier versions of this work. This research was supported by a Makerere University Grant for Biological Research; a University of Illinois Graduate College Fellowship; a Sigma Xi Grant-in-Aid-of-Research; and the University of Illinois, including a Department of Anthropology Summer Research Grant, a Center for African Studies Research Grant, and a Graduate College Thesis Support Grant. Finally, I thank Stephen Wooten for his encouragement, support, and patience during all phases of this research.

LITERATURE CITED

Augspurger CK. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. J Ecol 71:759–771.

Bailey BJR. 1980. Large sample simultaneous confidence intervals for the multinomial probabilities based on transformations of the cell frequencies. Technometrics 22:583–589.

Bourne GH, Golarez de Bourne MN. 1972. The histology and histochemistry of the chimpanzee tissues and organs. In: Bourne GH, editor. Histology, reproduction and restraint (volume 5): the chimpanzee. Baltimore: University of Park Press. p 2–76.

Chapman CA. 1988. Patterns of foraging and range use by three species of neotropical primates. Primates 29:177–194.

Chapman CA. 1989. Primate seed dispersal: the fate of dispersed seeds. Biotropica 21:148–154.

Chapman CA, Chapman LJ. 1995. Survival without dispersers: seedling recruitment under parents. Conserv Biol 9:675–678.

Chapman CA, Chapman LJ. 1996. Frugivory and the fate of dispersed and non-dispersed seed of six African tree species. J Trop Ecol 12:1–14.

Chapman CA, Wrangham RW. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. Am J Primatol 31:263–273.

Chapman CA, White FJ, Wrangham RW. 1994. Party size in chimpanzees and bonobos: a reevaluation of theory based on two similarly forested sites. In: Wrangham RW, McGrew WC, deWaal FB, Heltne PG, editors. Chimpanzee cultures. Cambridge, MA: Harvard University Press. p 41–58.

Chivers DJ. 1994. Functional anatomy of the gastrointestinal tract. In: Davies G, Oates JF, editors. Colobine monkeys: their ecology, behavior and evolution. Cambridge, UK: Cambridge University Press. p 205–228.

Chivers DJ, Raemakers JJ. 1986. Natural and synthetic diets of Malayan gibbons. In: Else JG, Lee PC, editors. Primate biology and conservation. Cambridge, UK: Cambridge University Press. p 39–56.

Cipollini ML, Levey DJ. 1997. Why are some fruit toxic? Glycoalkaloids in *Solanum* and fruits choice by vertebrates. Ecology 78:782–798.

Clemens ET, Maloiy GMO. 1981. Organic acid concentrations and digesta movement in the gastrointestinal tract of the bushbaby (*Galago crassicaudatus*) and vervet monkey (*Cercopithecus aethiops*). J Zool Lond 193:487–497.

Clemens ET, Phillips B. 1980. Organic acid production and digesta movement in the gastrointestinal tract of the baboon and sykes monkey. Comp Biochem Physiol 66:529–532.

Condit R, Hubbell SP, Foster RB. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. Am Nat 140:261–286.

Conklin NL, Wrangham RW. 1994. The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. Biochem Syst Ecol 22:137–151.

Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR, editors. Dynamics of populations. Dordrecht, The Netherlands: Center for Agricultural Publishing and Documentation. p 2948–3100.

Corlett RT. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. Biol Rev 73:413–448.

Corlett RT, Lucas PW. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fasicularis*). Oecologia 82:166–171.

Crawley MJ. 1992. Seed predators and plant population dynamics. In: Fenner M, editor. Seeds: the ecology of regeneration in plant communities. Melksham, UK: CAB International. p 157–192.
Davies G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. Int J Primatol 12:119–144.
Fenner M. 1992. Seeds: the ecology of regeneration in plant communities. Wallingford, UK: CAB International.
Fleagle JG. 1999. Primate adaptation and evolution. New York: Academic Press.
Fleming TH. 1988. The short-tailed fruit bat: a study in plant-animal interactions. Chicago: University of Chicago Press.
Frankie GW, Baker HG, Opler PA. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Int J Ecol 62:881–919.
Galdikas BM. 1982. Orang utans as seed dispersers at Tanjung Puting, Central Kalimantan: implications for conservation. In: Boer LEM, editor. The orang utan: its biology and conservation. The Hague: W. Junk Publishers. p 285–298.
Garber PA. 1986. The ecology of seed dispersal in two species of Callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). Am J Primatol 10:155–170.
Garber PA, Paciulli LM. 1997. Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). Folia Primatol (Basel) 68:236–253.
Gaulin SJC. 1979. A Jarman/Bell model of primate feeding niches. Hum Ecol 7:1–20.
Gautier-Hion A. 1980. Seasonal variation of diet related to species and sex in a community of *Cercopithecus* monkeys. J Anim Ecol 49:237–269.
Gautier-Hion A, Gautier J-P, Maisels F. 1993. Seed dispersal versus seed predation: an inter-site comparison of two related African monkeys. Vegetatio 107/108: 237–244.
Ghiglieri M. 1984. The chimpanzee of Kibale forest. New York: Columbia University Press.
Goodall J. 1986. The chimpanzees of Gombe. Cambridge, MA: Belknap Press of Harvard University Press.
Hamilton A. 1981. A field guide to Uganda forest trees. Kampala, Uganda: Makerere University Press.
Herrera CM. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. In: Estrada A, Fleming TH, editors. Frugivores and seed dispersal. Dordrecht, The Netherlands: Dr. W. Junk Publishers. p 5–18.
Howard PC. 1991. Nature conservation in Uganda's tropical forest reserves. Cambridge, UK: IUCN Tropical Forest Programme.
Howe HF. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539–550.
Howe HF. 1989. Scatter- and clump-dispersal and seedling demography: hypotheses and implications. Oikos 79:417–426.
Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228.
Howe HF, Vande Kerckhove GA. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology 62:1093–1106.
Howe HF, Westley LC. 1988. Ecological relationships of plants and animals. New York: Oxford Press.
Idani G. 1986. Seed dispersal by pygmy chimpanzees (*Pan paniscus*): a preliminary report. Primates 27:411–447.
Jacobsen N. 1970. Salivary amylase. II: alpha amylase in salivary glands of the *Macaca irus* monkey, the *Cercopithecus aethiops* monkey, and man. Caries Res 4:200–205.
Janzen DH. 1970. Herbivores and the number of tree species in tropical forest. Am Nat 104:501–528.
Janzen DH. 1971. Seed predation by animals. Annu Rev Ecol System 2:465–492.
Janzen DH. 1976. Two patterns of pre-dispersal seed predation by insects on Central American deciduous forest trees. In: Burley N, Styles J, editors. Tropical trees: variation, breeding, conservation. London: Linnaean Society. p 179–188.
Jones EG, Schwark HD, Callahan PA. 1986. Extent of the ipsilateral representation in the ventral posterior medial nucleus of the monkey thalamus. Exp Brain Res 63:310–320.
Julliot C. 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. Int J Primatol 17:239–258.
Kaplin BA, Moermond TC. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. Am J Primatol 45:83–102.
Kay RF, Sheine WS. 1979. On the relationship between chitin particle size and digestibility in the primate *Galago senegalensis*. Am J Phys Anthropol 50:301–308.
Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. Am J Phys Anthropol 81:5–15.
Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int J Primatol 14:207–228.
Lambert F. 1989. Some notes on fig eating by arboreal mammals in Malaysia. Primates 31:453–458.
Lambert JE. 1995. Redtail monkeys and *Strychnos mitis:* a plant-animal interaction in the Kibale forest, Uganda. Am J Primatol [Suppl] 35:32.
Lambert JE. 1997. Digestive strategies, fruit processing, and seed dispersal in the chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*) of Kibale National Park, Uganda. Ph.D. thesis. University of Illinois.
Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7:8–20.
Lambert JE. 1999. The fate of primate dispersed seeds. Am J Primatol [Suppl]. In press.
Lambert JE, Garber PA. 1998. Evolutionary and ecological implications of primate seed dispersal. Am J Primatol 45:9–28.
Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. Int J Primatol 14:257–314.
Levey DJ, Grajal A. 1991. Evolutionary implications of fruit-processing limitations in cedar waxwings. Am Nat 138:171–189.
Levey DJ, Karasov WH. 1994. Gut passage of insects by European starlings and comparison with other species. Auk 111:478–481.
Lucas PW. 1994. Categorization of food items for oral processing. In: Chivers DJ, Langer P, editors. The digestive system of mammals. Cambridge, UK: Cambridge University Press. p 197–218.
Lucas PW, Corlett RT. 1998. Seed dispersal by long-tailed macaques. Am J Primatol 45:29–44.
Lucas PW, Teaford MF. 1994. Functional morphology of colobine teeth. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behavior and evolution. Cambridge, UK: Cambridge University Press. p 173–204.

Maisels F. 1993. Gut passage rate in guenons and mangabeys: another indicator of a flexible dietary niche? Folia Primatol (Basel) 61:35–37.

Manger PR, Woods TM, Jones EG. 1995. Representation of the face and intra-oral structures in area 3b of the squirrel monkey (*Saimiri sciureus*) somatosensory cortex, with special reference to the ipsilateral representation. J Comp Neurol 362:597–607.

McKey DB. 1978. Soils, vegetation, and seed-eating by black colobus monkeys. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution Press. p 423–437.

Milton K. 1984. The role of food processing factors in primate food choice. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys and apes. New York: Columbia University Press. p 249–279.

Milton K, Demment MW. 1987. Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. J Nutr 118:1082–1088.

Moermond TC, Denslow JS. 1985. Neotropical frugivores: patterns of behavior, morphology, and nutrition with consequences for fruit selection. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG, editors. Neotropical ornithology. Washington, DC: AOU Monographs. p 865–897.

Murray P. 1973. The anatomy and adaptive significance of cheek pouches (bursae buccales) in the Cercopithecinae, Cercopithecoidea. Ph.D. thesis. Chicago: University of Chicago.

Murray P. 1975. The role of cheek pouches in cercopithecine monkey adaptive strategy. In: Tuttle RH, editor. Primate functional morphology and evolution. The Hague and Paris: Mouton Publishers. p 151–194.

Nagy KA, Knight MH. 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari desert. J Mamm 75:860–872.

Norconk MA, Grafton BW, Conklin-Brittain NL. 1998. Seed dispersal by neotropical seed predators. Am J Primatol 45:103–126.

Oftedal OT, Allen ME. 1996. The feeding and nutrition of omnivores with emphasis on primates. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity. Chicago: University of Chicago Press. p 148–158.

Phua PB, Corlett RT. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). Malay Nat J 42:251–256.

Rahaman H, Srihari K, Krishnamoorthy RV. 1975. Polysaccharide digestion in cheek pouches of the bonnet macaque. Primates 16:175–180.

Rowell TE, Mitchell BJ. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. J Trop Ecol 7:269–274.

Rudran R. 1978. Socioecology of the blue monkeys of the Kibale forest, Uganda. Smithsonian contributions to zoology, 249. Washington, DC: Smithsonian Institution Press.

Sailer LD, Gaulin SJC, Boster JS, Kurland JA. 1985. Measuring the relationship between dietary quality and body size in primates. Primates 26:14–27.

Schoener TW. 1971. Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404.

Schupp EW. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. In: Fleming TH, Estrada A, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Boston: Kluwer Academic Publishers. p 15–30.

Snow BK, Snow DW. 1988. Birds and berries. Calton, UK: T. & A.D. Poyser Publishers.

Sorenson AE. 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). J Anim Ecol 53:545–557.

Stiles EW. 1989. Fruits, seeds, and dispersal agents. In: Abrahamson WG, editor. Plant-animal interactions. New York: McGraw-Hill. p 87–122.

Struhsaker TT. 1975. The red colobus monkey. Chicago: University of Chicago Press.

Struhsaker TT. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. Gainesville, FL: University Press of Florida.

Takasaki H. 1983. Seed dispersal by chimpanzees: a preliminary note. Afr Stud Monogr 3:105–108.

Tutin CEG, Williamson EA, Rogers ME, Fernandez M. 1991. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon. J Trop Biol 7:181–199.

Ungar PS. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. Am J Phys Anthropol 95:197–219.

Ungar PS. 1995. Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. Int J Primatol 16:221–245.

Van Roosmalen MGM. 1984. Subcategorizing foods in primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 167–176.

Van Schaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377.

Walker PL. 1979. The adaptive significance of pongid lip mobility. Int J Skel Res OSSA 6:277–283.

Warner ACI. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutr Abstr Rev [B] 51:789–820.

Waterman PG. 1984. Food acquisition and processing as a function of plant chemistry. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p 177–212.

Waterman PG, Kool K. 1994. Colobine food selection and plant chemistry. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behavior and evolution. Cambridge, UK: Cambridge University Press. p 251–284.

Whitten AJ. 1982. Diet and feeding ecology of Kloss gibbons on Siberut Island, Indonesia. Folia Primatol (Basel) 37:177–208.

Whitmore TC. 1990. An introduction to tropical rain forests. Oxford, UK: Clarendon Press.

Willson MF, Whelan CJ. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season, and species. Oikos 57:191–198.

Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP. 1993. The value of figs to chimpanzees. Int J Primatol 14:243–256.

Wrangham RW, Chapman CA, Chapman LJ. 1994. Seed dispersal by forest chimpanzees in Uganda. J Trop Ecol 10:355–368.